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## An overview of research from a high elevation landscape: the Niwot Ridge, Colorado Long Term Ecological Research programme

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**Background:** There is a paucity of information for mountain catchments, and in particular a lack of long-term data collection in alpine areas.

**Aims:** The focus of this special issue is to synthesize alpine research undertaken in the last 20 years at high altitude research sites that comprise the Niwot Ridge Long Term Ecological Research (NWT LTER) programme. It is a timely update of the benchmark volume on alpine ecology by Bowman and Seastedt (2001) that presented a summary of work carried out over 40 years on the structure and functioning of the NWT LTER alpine terrestrial and aquatic ecosystems.

**Methods:** We introduce and synthesize both the individual manuscripts in this monograph, along with insights from non-LTER investigators.

**Results and conclusions:** Mountain areas are sentinels of climate change. We are seeing those effects today. Furthermore, these ecosystem changes we report are occurring in mountain areas before they occur in downstream ecosystems. Thus, the sensitivity of mountain ecosystems to changes in climate begs for enhanced and worldwide protection. Our results suggest that investing in observational and integrated social-ecological system research in mountains is key for underpinning scientifically the development and implementation of efficient mitigation and adaptation measures and sustainable development strategies.

**Keywords:** alpine environments; alpine ecology; alpine tundra; cryosphere; hydrology; Niwot Ridge; snow distribution; snow chemistry

### Introduction

The components of high elevation landscapes – characteristic glacial geomorphology with mountain peaks, glaciers and lakes carved by a past climate and vegetation features that include treeline and treeline ecotone and alpine ecosystems – are among the least impacted by humans (Figure 1). In our time, the belief that “mountains are forever” has provided inspiration and comfort to those seeking stability in a rapidly changing world (Seastedt et al. 2004). However, changes in the hydrology and in the abundance and species composition of the native flora and fauna of mountain ecosystems are potential bellwethers of global change. While recent studies have continued to show that these systems have a remarkable propensity to amplify environmental changes within specific portions of this landscape, the opposite is also true. A portion of the alpine environment and its ecosystems are resilient to changes, but this resilience is subject to climatic controls that may be changing.

In the time since previous summaries of our understanding of the structure and functioning of the alpine ecosystems at Niwot Ridge, Colorado were presented (Bowman and Seastedt 2001), the importance of the sensitivity of ecosystems to global change drivers has been affirmed across the world, and the alpine belt of mountains

is not immune to these changes. The physical and biological consequences of the presence and amounts of snow received by the alpine elevations are large in extratropical latitudes, and these consequences will change if precipitation inputs change in quantity or occur as rain rather than snow (Seastedt et al. 2004; Robertson et al. 2012). There is evidence to indicate that changes in the seasonality, amounts, and type (e.g. rain or snow) of precipitation, as mediated by temperature, are underway (Bavay et al. 2009). Understanding how changes in atmospheric chemistry, climate, introduced species and other global change drivers may affect mountain environments crosses many disciplines and requires contributions from the atmospheric sciences, biogeosciences, hydrology, remote sensing, ecology, economics and other dimensions within the natural and social sciences.

Changes in mountain regions will affect much of humanity, as more than one-sixth of the world's population lives in river basins fed by snow or glacier melt, and thus seasonal shifts in stream flow and possibly reduced low flows caused by glacial retreat or decreased snow water storage are likely to adversely affect ecosystem structure and functioning, derived ecosystem services and related human activities, particularly in semiarid regions. As a result, we must improve our understanding of how

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Figure 1. The Colorado Front Range, the easternmost boundary of the North American Continental Divide, as viewed from near the treeline on Niwot Ridge (photo by Jeff Mitton).

hydrologic processes, biogeochemical cycling, and species distribution, abundance, and functioning in high elevation catchments will respond to a combination of changes in climate, atmospheric deposition of pollutants such as ammonium and nitrate (= dissolved inorganic nitrogen, DIN), and potential changes in the quantity and chemistry of dust deposition. Small changes in the flux of energy, chemicals, and water to high elevation environments may invoke large changes in mountain climate, ecosystem dynamics, and water quantity and quality (Williams et al. 2002). Improved knowledge of the processes controlling feedback will promote clearer understanding of Earth's water, energy and biogeochemical cycles and enable sounder management of increasingly these stressed natural resources (Bales et al. 2006). However, our knowledge of these processes is limited by a lack of adequate understanding and long-term surveillance of physical and biogeochemical processes, driven by logistical constraints associated with high elevation environments, including cold air temperatures, blowing snow and low oxygen partial pressures and access problems in winter in seasonal climates (Williams et al. 1999). Collectively, these generate physiologically demanding conditions that, in theory at least, alter biotic functions.

There is thus a paucity of information for mountain catchments, and in particular a lack of long-term data collection in alpine areas. Niwot Ridge is a major multidisciplinary, long-term field site representing high elevation areas on the North American continent. Only a few other North American sites are in existence (e.g. White Mountain Research, the Loch Vale Watershed, and the Rocky Mountain Research Laboratory) that routinely conduct high elevation research. As such, research at Niwot Ridge provides a crucial reference point for regional, national and global networks that measure geophysical

and biological changes and feedback, and that experimentally assess the mechanisms involved in these relationships.

Human-driven changes to the global environment – including climate, atmospheric composition, nutrient cycles, hydrologic cycling, and ecosystem structure – are now pervasive throughout the world and continue to accelerate (e.g. IPCC 2007; Steffen et al. 2007; Galloway et al. 2008). While such changes have brought substantial benefits to humanity (e.g. Smil 2001; Kareiva et al. 2007; Townsend and Howarth 2010), they increasingly cause detrimental outcomes for both people and ecosystems (Galloway et al. 2008; Carpenter et al. 2009), including those in and around the Niwot Ridge Long Term Ecological Research (NWT LTER) site (Steltzer and Bowman 1998; Williams and Tonnessen 2000; Bowman et al. 2006). Indeed, while some portions of high elevation ecosystems are often free of direct transformation via land use change (Bourgeron et al. 2009), taken as a whole, alpine vegetation and montane forests have been identified as particularly sensitive to the suite of human-induced environmental changes that currently challenge society (Williams et al. 2002; IPCC 2007; Langdon and Lawler 2015).

The focus of this special issue is to synthesise research undertaken in the last 20 years at high altitude research sites that comprise the NWT LTER (Figure 2). It is a timely update of the benchmark volume on alpine ecology by Bowman and Seastedt (2001) that presented a summary of work carried out during the preceding 40 years on the structure and functioning of the Niwot Ridge alpine terrestrial and aquatic ecosystems. In this Niwot Ridge monograph, the focus is on aspects of temporal changes in the abiotic system and ecosystem structure and functioning, and on reporting new kinds of research and synthesis that have been developed since 1995.

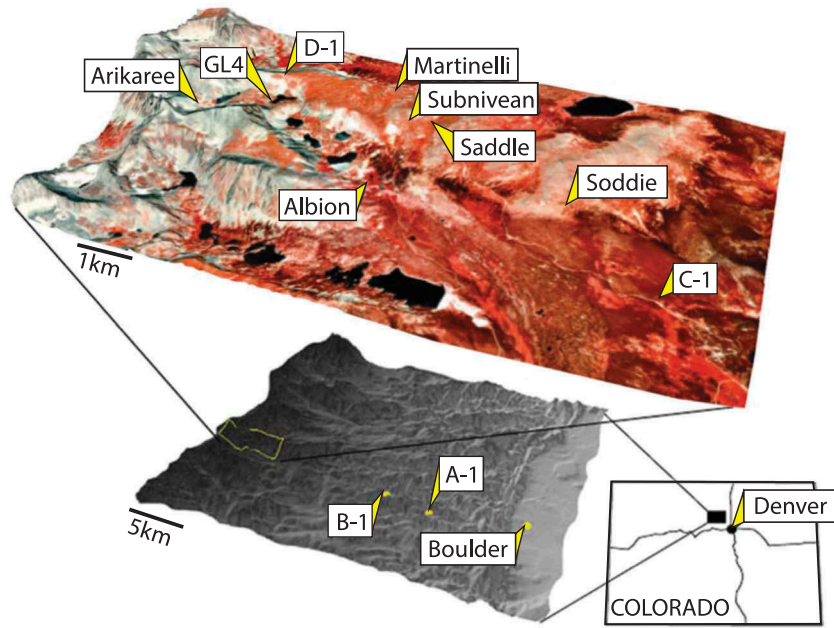


Figure 2. Study locations within the Niwot Ridge LTER area.

### Research at the NWT LTER

The NWT LTER site, the only alpine site in the US National Science Foundation sponsored LTER network, is located in the Colorado Front Range and extends to the Continental Divide (Figure 2). Long-term monitoring at Niwot Ridge began in the 1950s with the installation of meteorological stations at a subalpine forest site (termed C1) located at 3005 m, and an alpine site (termed D1) located at 3739 m. The D1 site represents the longest high elevation climate record in the US. Building on research activities and insights up to 1995, we began to investigate the propensity of high elevation areas to amplify environmental changes and to examine the potential of high elevation ecosystems to accumulate and redistribute exogenous materials from the atmosphere and endogenous materials from the mountains. This analysis led us to a conceptual model of the coupled relationships among high elevation ecosystems that emphasises the importance of transport processes – the Landscape Continuum Model (LCM) of Seastedt et al. (2004). We also expanded our research area from the alpine zone to include the down-gradient subalpine forest area in the Como Creek drainage (Figure 1). Indeed, the term “subalpine” implies a relationship with the alpine that in many ways does appear to be more substantial than ecotones found between many herbaceous and forested systems. In the following paragraphs, we highlight the studies undertaken as part of the NWT LTER programme, including those papers presented in this monograph, emphasising specific recent findings.

The presence of a seasonal snowpack in extratropical mountain environments may amplify climate signals because of impacts related to the redistribution, storage and release of melt water, solutes and particulates from snow (Seastedt et al. 2004). Moreover, meteorological,

hydrological, cryospheric and ecological conditions change greatly over relatively short distances in high mountain environments because of their rugged terrain, and thus the boundaries between different ecological zones in the alpine are sensitive to small environmental changes. In the past, we have noted that the harsh conditions characteristic of these environments suggested that some organisms in high mountain ecosystems are on the razor’s edge of tolerance (Williams et al. 2002). Yet, with notable exceptions, such as the pika (*Ochotona princeps*) (Ray et al. 2015), this may not be a generality; there appear to be winners as well as losers in these interactions, and discovering which of the organisms and the biogeochemical processes mediated by them in high elevation catchments are sensitive to small changes in climate and other environmental parameters is an important activity.

At the level of organismic biology, the alpine belt possesses iconic species such as the pika, a mammalian lagomorph, which has been identified as one of the first potential victims of climate change (Holtcamp 2010). Vegetation includes a mix of species, some of which appear sensitive to very small changes in DIN (Bowman et al. 2012). Our alpine studies at Niwot Ridge includes findings that argue that portions of the vegetation in this landscape appear relatively stable (e.g. Spasojevic et al. 2013), yet at the same time we cannot dismiss the notion that much of the alpine belt may be vulnerable to what could be viewed as a true vegetation transformation, the conversion of a predominantly herbaceous (graminoid and forb) system to one dominated by shrubs (Formica et al. 2014). An emerging field involves documenting the positive and negative interactions among plants, microbes, and soils in the alpine belt, with findings indicating strong connections between plant and microbial community



composition and their biogeochemical functions (Farrer et al. 2013; Dean et al. 2014).

### Atmospheric interactions and biogeochemistry

Since 1996, the NWT LTER programme has become a leader in biogeochemical cycling under the seasonal snowpack (Brooks et al. 1996, 1997, 1998; Schadt et al. 2003), and we continued that research tradition with a special issue of Biogeochemistry (Williams et al. 2009a). For this special issue, we emphasised our new insights into microbial/biogeochemical/vegetation interactions (Schmidt et al. 2014; Liptzin et al. 2015). We developed a novel *in situ* experimental system at a treeline area (the Soddie site) at the 3340 m site in the Como Creek drainage. At this site trace gases were/have been continuously sampled at hourly time-steps from above and within the snowpack for the duration of seasonal snow cover (Seok et al. 2009), and provided additional insights into microbial controls on trace gas fluxes (Liptzin et al. 2015). We built on this new expertise in measuring trace gas fluxes by deploying an eddy covariance (EC) system in a dry meadow type alpine vegetation to provide a direct measure of water vapour and carbon dioxide fluxes between the biosphere and the atmosphere. By combining these results with a second EC tower in the subalpine forest at C1, we were able to synthesise these studies into a catchment-scale model of water and carbon cycling, within the context of regional disturbance and environmental change (Knowles et al. 2015). Finally, the role of dust and particulate matter originating outside of the high elevation region, a factor noted by Litaor (1987), has undoubtedly increased in importance and is influencing snow duration and water chemistry (Mladenov et al. 2012; Brahney et al. 2013; Goss et al. 2013; Lawrence et al. 2013).

These synthesis activities were made possible through the combination of long-term monitoring, long-term experiments, process-based research activities, and punctuated disturbances. Our long-term data on climate and nitrogen (N) deposition exhibit directional trends that exceed historical ranges of variability and we hypothesise that are pushing our high elevation ecosystems into new states not shown in the historical record (Bowman et al. 2015). For example, 45 years of glacial mass balance and climate data show that recent increases in summer air temperature have resulted in the mass balance of the Arikaree Glacier crossing a threshold from stable over the last 40 years to a large negative mass balance that will most likely result in the disappearance of the glacier in the next two decades (Leopold et al. 2015). Deposition of DIN in wetfall has increased by a factor of three over the last two decades, causing the Green Lakes Valley watershed (dominated by barren soils with little vegetation) to switch from an N-limited state to what can be considered an N-saturated system (Williams et al. 1996) that is now phosphorus (P) limited (Elser et al. 2009a, 2009b). By contrast, most alpine plant communities on Niwot Ridge are still N-limited

(Williams et al. 2009b), but are reaching a tipping point because N deposition has reached critical loads (Bowman et al. 2006, 2015; Suding et al. 2008).

To emphasise how our research foci tie together conceptually, our NWT LTER overarching hypothesis in 2011 stated that changes in the amount and timing of snow and snowmelt, along with increasing N deposition and increasing dust deposition, and punctuated disturbance, such as the mountain pine beetle outbreak, will decrease hydrologic connectivity among landscapes, leading to decreased biodiversity, less heterogeneity of high elevation landscapes and a decrease in important ecosystem services (Figure 3). Hydrological connectivity is driven by the duration and timing of the seasonal snowpack and snowmelt, and under a warming climate, increasing windborne dust will accelerate snowpack and glacial melt, which will result in the snowline moving to a higher elevation, which will, in turn, decrease hydrological connectivity (Robertson et al. 2012). With elevated N inputs from windborne dust, we believe that in some communities, plant species diversity will decrease as alpine areas shrink, shrublands will expand, and the landscape will become more homogeneous. Treeline will likely advance in at least some habitats where winds and moisture limitations, factors somewhat independent of warming, allow the existence of the tree life form (Bourgeron et al. 2016).

Our research shows that surface/groundwater interactions are an important component of water quantity and quality in alpine basins (Williams et al. 2015). Thus alpine basins are not “Teflon basins”; some or most snowmelt infiltrates underlying soils and bedrock, transporting soil and bedrock products to surface waters. The increase in atmospheric DIN has caused an increase in net nitrification in soils. Infiltrating snowmelt, along with increased melt of stored ice, increases the hydrologic connectivity between the terrestrial and aquatic systems. Nitrate, dissolved organic carbon (DOC) and nitrogen (DON) are thus flushed from soils and talus to streams. These results show that alpine catchments, such as GL4 (Figure 2), have the greatest sensitivity and least resilience to climate warming, with any warming leading to increased water yields. Cryospheric change and its consequences are manifest themselves as long-term trends that in many places will be difficult to discern from short-term variability in climate and other environmental factors and in social dynamics, such as population and economic change. Long-term alpine research sites, such as the NWT LTER provide the perspective necessary to detect trends in mountain environments that would otherwise not be visible against this variability (Robertson et al. 2012).

### Organismic and community ecology

The pika is the iconic North American alpine mammal and a charismatic poster-child for climate change. Work by Bhattacharyya and Ray (2015) notes how climate change becomes a double-threat to pikas, i.e. their habitats are

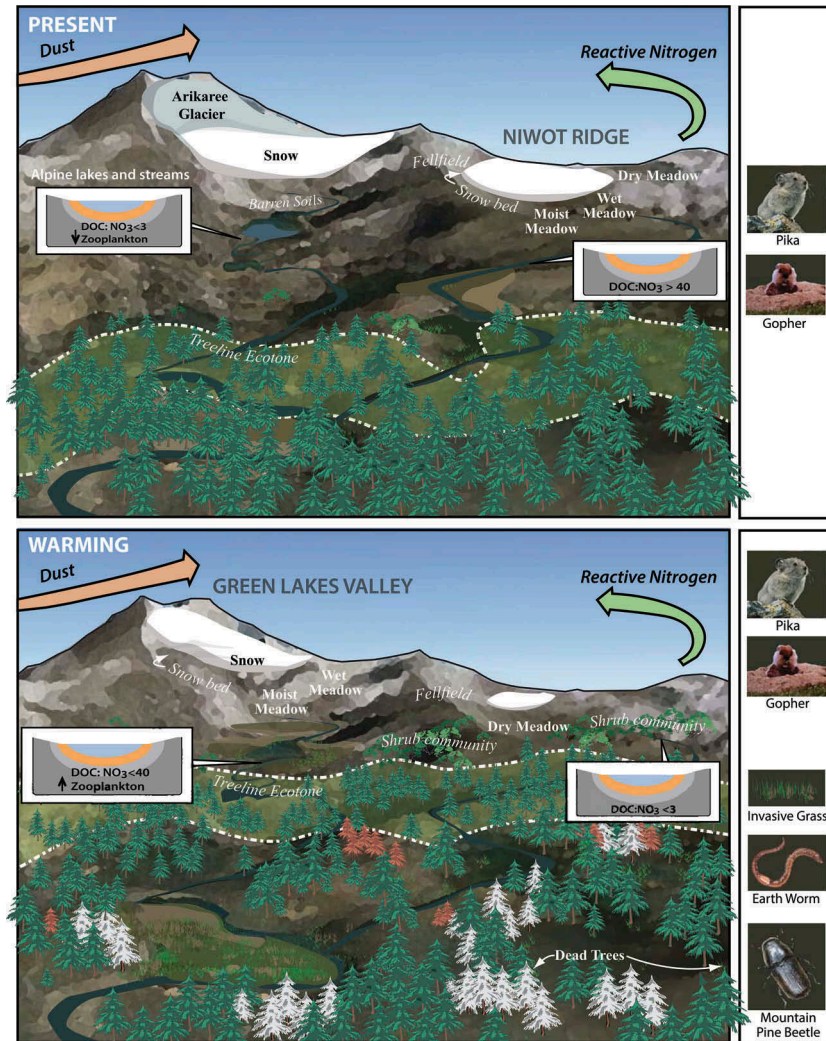


Figure 3. Graphical representation of environmental drivers and ongoing changes at Niwot Ridge. Adapted from Robertson et al. (2012).

becoming both too cold in spring and autumn because of reduced snow duration/cover and too hot during the summer when these animals build up their food caches for winter; these cause the energy balance of these animals to suffer as a result. This work also emphasises the extreme heterogeneity in climate conditions found in the alpine, a story that has driven our plant community ecology for decades. The pika is perhaps unique in that these changes in population dynamics are based simply on changes in the energy balance of the organism as a consequence of warming or less snow cover. While indirect effects on resources, predators, and pathogens may be involved, these have not been identified.

Studies of other consumers found in the alpine belt have been relatively few at Niwot Ridge in this century. Since the summary of vertebrate studies by Armstrong et al. (2001), occasional live trapping of mammals has been undertaken on Niwot Ridge, but no new reports have been produced. One invertebrate group of potential

interest, grasshoppers, were studied in the 1990s (Coxwell and Bock 1995). The changes in the species composition and abundance of grasshopper species over a 50-year period have been summarised for a treeline ecotone meadow at about 3050 m elevation (Buckley et al. 2015). Such studies are bellwethers of the future studies, which will require information on changes of both the biotic and abiotic environments of the target organisms in order to interpret climate change responses.

Gophers, the burrowing rodents that function as ecosystem engineers of the alpine (Sherrod and Seastedt 2001; Sherrod et al. 2005) have, to our knowledge, not shown major directional changes in activities in recent decades. However, their local populations are so variable in terms of density that identifying such a response is going to be difficult, but their activities are generally associated with soils that rarely freeze. Warming, either directly or through changes in the seasonality of snow cover, should expand the range of habitats available to these animals. However, the

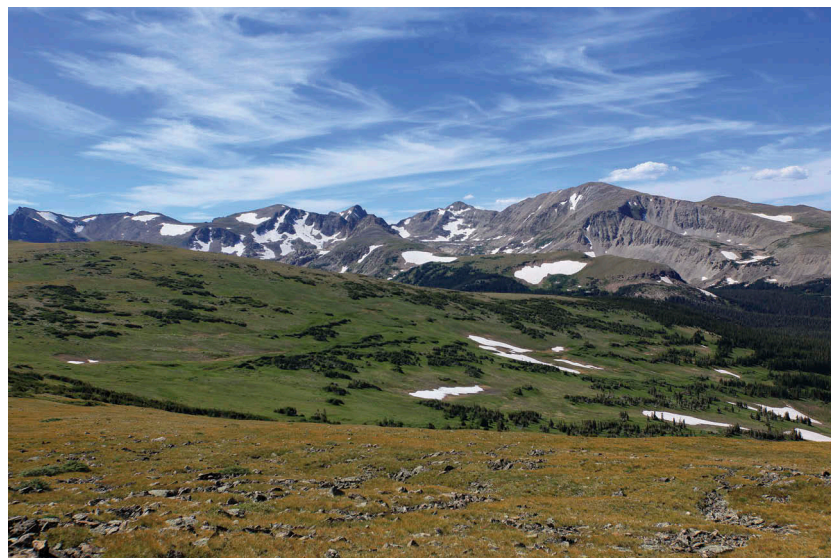


Figure 4. Treeline is under multiple controlling factors at Nivot Ridge. Temperature controls are moderated by wind scour and snow avalanches. Ribbon forests sometimes form above the zone of continuous forest (photo by Jeff Mitton).

concurrent increases in abundances of their less preferred food supply, the graminoids (Bowman et al. 2015) or shrubs (Formica et al. 2014), may constrain population growth and increases in available habitat for this species.

Understanding the dynamics of alpine plant communities remains very much an interest and research strength of the NWT LTER programme. Documentation of the very real impacts of N deposition (DIN) remains a focus (Bowman et al. 2015), while plant community dynamics have been studied through a series of experiments that manipulate biotic resource interactions (Ashton et al. 2008; Suding et al. 2008; Farrer et al. 2015; Gasarch and Seastedt 2015a, 2015b). Among these studies are those that attempt to understand community feedback on soil characteristics, including changes in carbon sequestration resulting from changes in snow depth and duration or N inputs (Freppaz et al. 2012). Incorporating plant–microbial interactions has been an emerging strength of this effort (Farrer et al. 2013; Dean et al. 2014; Yuan et al. Forthcoming). These studies provide a new dimension of an alpine microbial ecology programme that has emphasised microbial biodiversity as well as ecological relationships of these organisms (Ley et al. 2004; Schmidt et al. 2014). The role that plants and microbes play in the colonisation of the high alpine-subnival regions is also an area of active research (King et al. 2012). We suspect that this dance between microbial and plant communities also occurs at treeline or in ribbon forests (as shown in Figure 4), and plant–microbial interaction studies are ongoing.

Nested within the long-term study of hydrology and biogeochemistry of high elevation surface waters, the lake studies conducted by McKnight and colleagues continue to document the sensitivity of the aquatic biotic components to changes affecting the high elevation watersheds (Miller and McKnight 2015). The lake biota, as

represented by the phytoplankton, appears to be very sensitive to DIN and other factors affecting water quality. And, as noted for the terrestrial communities, transformations in the communities associated with changes in the limiting resources have occurred and are underway.

### Education and outreach

The NWT LTER programme was one of the first to develop a children's book to communicate the importance of the alpine environments to society. *My Water Comes From the Mountains* (Fourment 2004) has been used and modified across the western US. The attraction of the alpine world to non-scientists has not diminished, and the potential to use the popularity of this ecosystem as a natural laboratory to educate primary and secondary students (K-12) and the public about societally relevant changes remains an important aspect of the NWT LTER programme.

We place these results and new insights into the framework of environmental science literacy – the capacity to participate in and make decisions through evidence-based discussions of socio-ecological systems – which is essential not only for many science careers but also for responsible citizenship (Robertson et al. 2012). The development of an environmental science literacy framework is crucial for providing this capacity among K-12 students, a key constituency that represents future science, technology, engineering and mathematics professionals and the 75% of the US population that will not earn a higher degree. As noted by Ray et al. (2015), the LTER outreach effort has integrated scientific principals in a way that develops a level of environmental appreciation that can lead to life-long learning to support the ecosystem services needed to maintain and enhance human well-being.



## Summary

Mountain areas are thus sentinels of climate change. We are seeing the effects of climate change on both abiotic (hydrology) and biotic (shrub expansion) systems in the alpine today. Furthermore, these ecosystem changes are occurring in mountain areas before they occur in downstream ecosystems. Thus, the sensitivity of mountain ecosystems begs for enhanced protection and worldwide protection. Our understanding of the processes that control mountain ecosystems – climate interactions, snowmelt runoff, biotic diversity, nutrient cycling – is much less developed compared to downstream ecosystems where human habitation and development has resulted in large investments in scientific knowledge to sustain health and agriculture.

Given these results from the NWT LTER programme and the global societal relevance of mountain regions, it is necessary to quantify how global change drivers impact the entire socio-ecological system in mountains, with particular focus on the water cycle, ecosystems and biodiversity and their uses by humans. This requires a network of mountain research and monitoring stations spanning the most important mountain ranges so that issues common to all mountain areas as well as issues of regional importance can be identified and solutions developed. Our results suggest that investing in observational and integrated social-ecological system research in mountains is key for underpinning scientifically the development and implementation of efficient mitigation and adaptation measures and sustainable development strategies.

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## Disclosure statement

No potential conflict of interest was reported by the authors.

## Notes on contributors

Mark Williams is a hydrologist; he is interested in mountain ecology and hydrology. He was Principal Investigator of the NWT LTER programme between 2004 and 2014.

Timothy R. Seastedt is an ecologist with diverse interests in terrestrial ecosystems, including the mechanisms driving biotic change in the Anthropocene. He was the Principal Investigator of the NWT LTER programme from 1992–2004.

William Bowman is a professor specialising in plant community ecology in alpine areas. He is Director of the Mountain Research Station and his research interests and recent publications can be found at <http://www.colorado.edu/bowmanlab>

Diane McKnight is a professor of Civil, Environmental, and Architectural Engineering at the University of Colorado, Boulder. Her research focuses on interactions between hydrologic, chemical and biological processes in controlling the dynamics in aquatic ecosystems.

Katharine Suding is an ecologist whose research is focused on vegetation change, plant soil feedback and non-linear dynamics. She has worked at Niwot Ridge for over a decade, and is Principal Investigator of the NWT LTER programme.

## References

- Armstrong DM, Halfpenny JC, Southwick CH. 2001. Vertebrates. In: Bowman WD, Seastedt TR, editors. Structure and function of an alpine ecosystem. Oxford: Oxford University Press; p. 128–156.
- Ashton IW, Miller AE, Bowman WD, Suding KN. 2008. Nitrogen preferences and plant-soil feedbacks as influenced by neighbors in the alpine tundra. *Oecologia* 156:625–636.
- Bales R, Molotch NP, Painter TH, Dettinger MD, Rice R, Dozier J. 2006. Mountain hydrology of the western United States. *Water Resources Research* 42:W08432. doi:10.1029/2005WR004387.
- Bavay M, Lehning M, Jonas T, Lowe H. 2009. Simulations of future snow cover and discharge in alpine headwater catchments. *Hydrological Processes* 23:95–108.
- Bhattacharyya S, Ray C. 2015. Of plants and pikas: evidence for a climate-mediated decline in forage and cache quality. *Plant Ecology & Diversity* 8: This volume.
- Bourgeron P, Humphries H, Liptzin D, Seastedt TR. 2016. The forest-alpine tundra ecotone: a multiscaled approach to spatial and temporal dynamics of change at Niwot Ridge. *Plant Ecology & Diversity* (this issue). doi:10.1080/17550874.2015.1126368
- Bourgeron PS, Humphries HC, Riboli-Sasco L. 2009. Regional analysis of social-ecological systems. *Natures Sciences Sociétés* 17:185–193.
- Bowman WD, Gartner JR, Holland K, Wiedermann M. 2006. Nitrogen critical loads for alpine vegetation and terrestrial ecosystem response: are we there yet? *Ecological Applications* 16:1183–1193.
- Bowman WD, Murgel J, Blett T, Porter E. 2012. Nitrogen critical loads for alpine vegetation and soils in Rocky Mountain National Park. *Journal of Environmental Management* 103:165–171.
- Bowman WD, Nemergut DR, McKnight DM, Miller MP, Williams MW. 2015. A slide down a slippery slope – alpine ecosystem responses to nitrogen deposition. *Plant Ecology & Diversity*. doi:10.1080/17550874.2014.984786
- Bowman WD, Seastedt TR, editors. 2001. Structure and function of an alpine ecosystem. Oxford: Oxford University Press.
- Brahney J, Ballantyne AP, Sievers C, Neff JC. 2013. Increasing Ca<sup>2+</sup> + deposition in the western US: the role of mineral aerosols. *Aeolian Research* 10:77–87. doi:10.1016/j.aeolia.2013.04.003
- Brooks PD, Schmidt SK, Williams MW. 1997. Winter production of CO<sub>2</sub> and N<sub>2</sub>O from alpine tundra: environmental controls and relationship to inter-system C and N fluxes. *Oecologia* 110:403–413.
- Brooks PD, Williams MW, Schmidt SK. 1996. Microbial activity under alpine snowpacks, Niwot Ridge, Colorado. *Biogeochemistry* 32:93–113.
- Brooks PD, Williams MW, Schmidt SK. 1998. Inorganic nitrogen and microbial biomass dynamics before and during spring snowmelt. *Biogeochemistry* 43:1–15.
- Buckley LB, Nufio CR, Kirk EM, Kingsolver JG. 2015. Elevational differences in developmental plasticity determine



- phenological responses of grasshoppers to recent climate warming. *Proceedings of the Royal Society B: Biological Sciences*. 282:20150441.
- Carpenter SR, Mooney HA, Agard J, Capistrano D, DeFries RS, Diaz S, Dietz T, Duraipappah AK, Oteng-Yeboah A, Pereira HM, et al. 2009. Science for managing ecosystem services: beyond the millennium ecosystem assessment. *Proceedings of the National Academy of Sciences of the United States of America*. 106:1305–1312.
- Coxwell CC, Bock CE. 1995. Spatial variation in diurnal surface temperatures and the distribution and abundance of an alpine grasshopper. *Oecologia* 104:433–439.
- Dean SL, Farrer EC, Taylor DL, Porras-Alfaro A, Suding KN, Sinsabaugh RL. 2014. Nitrogen deposition alters plant–fungal relationships: linking belowground dynamics to aboveground vegetation change. *Molecular Ecology* 23:1364–1378.
- Elser JJ, Andersen T, Baron JS, Bergstrom A-K, Jansson M, Kyle M, Nydick KR, Steger L, Hessen DO. 2009a. Shifts in lake N:P stoichiometry and nutrient limitation driven by atmospheric nitrogen deposition. *Science* 326:835–837.
- Elser JJ, Kyle M, Steger L, Nydick KR, Baron JS. 2009b. Nutrient availability and phytoplankton nutrient limitation across a gradient of atmospheric nitrogen deposition. *Ecology* 90:3062–3073.
- Farrer EC, Ashton IW, Spasojevic MJ, Fu S, Gonzalez DJ, Suding KN. 2015. Indirect effects of global change accumulate to alter plant diversity but not ecosystem function in alpine tundra. *Journal of Ecology* 103:351–360.
- Farrer EC, Herman DJ, Franzova E, Pham T, Suding KN. 2013. Nitrogen deposition, plant carbon allocation, and soil microbes: changing interactions due to enrichment. *American Journal of Botany* 100:1458–1470.
- Formica A, Farrer EC, Ashton IW, Suding KN. 2014. Shrub expansion over the past 62 years in Rocky Mountain alpine tundra: possible causes and consequences. *Arctic, Antarctic, and Alpine Research* 46:616–631.
- Fourment T. 2004. My water comes from the mountains. Lanham (MD): Roberts Rinehart.
- Freppaz M, Williams MW, Seastedt T, Filippa G. 2012. Response of soil organic and inorganic nutrients in alpine soils to a 16-year factorial snow and N-fertilization experiment, Colorado Front Range, USA. *Applied Soil Ecology* 62:131–141.
- Galloway JN, Townsend AR, Erismann JW, Bekunda M, Cai ZC, Freney JR, Martinelli LA, Seitzinger SP, Sutton MA. 2008. Transformation of the nitrogen cycle: recent trends, questions, and potential solutions. *Science* 320:889–892.
- Gasarch EI, Seastedt TR. 2015a. Plant community resilience to nitrogen and phosphorus enrichment varies across an alpine tundra moisture gradient. *Plant Ecology & Diversity* 8: This volume.
- Gasarch EI, Seastedt TR. 2015b. The consequences of multiple resource shifts on the community composition of alpine tundra: inferences from a long-term snow and nutrient experiment. *Plant Ecology & Diversity* 8: This volume.
- Goss N, Mladenov N, Seibold C, Chowanski K, Seitz L, Wellemeyer TB, Williams MW. 2013. Quantifying particulate matter deposition in Niwot Ridge, Colorado: Collection of dry deposition using marble inserts and particle imaging using the FlowCAM, *Atmospheric Environment*, 80:549–558.
- Holtcamp W. 2010. Silence of the pikas. *BioScience* 60:8–12.
- IPCC. 2007. Climate Change 2007: Impacts, Adaptation and Vulnerability. In: Parry ML, Canziani OF, Palutikof JP, van der Linden PJ, Hanson CE, editors. Contribution of Working Group II to the fourth assessment report of the Intergovernmental Panel on Climate Change. Cambridge (UK): Cambridge University Press.
- Kareiva P, Watts S, McDonald R, Boucher T. 2007. Domesticated nature: shaping landscapes and ecosystems for human welfare. *Science* 316:1866–1869.
- King AJ, Farrer EC, Suding KN, Schmidt SK. 2012. Co-occurrence patterns of plants and soil bacteria in the high-alpine subnival zone track environmental harshness. *Frontiers in Microbiology* 3:347–347.
- Knowles JF, Burns SP, Blanken PD, Monson RK. 2015. Fluxes of energy, water, and carbon dioxide from mountain ecosystems at Niwot Ridge, Colorado. *Plant Ecology & Diversity* 8: doi:10.1080/17550874.2014.904950
- Langdon JG, Lawler JJ. 2015. Assessing the impacts of projected climate change on biodiversity in the protected areas of western North America. *Ecosphere* 6:art87.
- Lawrence CR, Reynolds RL, Ketterer ME, Neff JC. 2013. Aeolian controls of soil geochemistry and weathering fluxes in high-elevation ecosystems of the Rocky Mountains, Colorado. *Geochimica Et Cosmochimica Acta* 107: 27–46.
- Leopold M, Lewis G, Dethier D, Caine N, Williams MW. 2015. Cryosphere: ice on Niwot Ridge and in the Green Lakes Valley, Colorado Front Range. *Plant Ecology & Diversity* 8: doi:10.1080/17550874.2014.992489
- Ley RE, Williams MW, Schmidt SK. 2004. Microbial population dynamics in an extreme environment: controlling factors in talus soils at 3750 m in the Colorado Rocky Mountains. *Biogeochemistry* 68:297–311.
- Liptzin D, Helmig D, Schmidt SK, Seok B, Williams MW. 2015. Winter gas exchange between the atmosphere and snow-covered soils on Niwot Ridge, Colorado, USA. *Plant Ecology & Diversity* 8. doi:10.1080/17550874.2015.1065925
- Litaor M. 1987. The influence of eolian dust on the genesis of alpine soils in the Front Range, Colorado. *Soil Science Society of America Journal*. 51:142–147.
- Miller MP, McKnight DM. 2015. Limnology of the Green Lakes Valley: phytoplankton ecology and dissolved organic matter biogeochemistry at a long-term ecological research site. *Plant Ecology & Diversity* 8. doi:10.1080/17550874.2012.738255
- Mladenov N, Williams MW, Schmidt SK, Cawley K. 2012. Atmospheric deposition as a source of carbon and nutrients to an alpine catchment of the Colorado Rocky Mountains. *Biogeosciences* 9:3337–3355.
- Ray C, McKnight DM, Bidwell MD, Fourment T, Flanagan-Pritz C, Rinehart AH. 2015. Children's book series and associated curricula support elementary education and outreach in water resources. *Plant Ecology & Diversity* 8. doi:10.1080/17550874.2015.1050711
- Robertson GP, Collins SL, Foster DR, Brokaw N, Ducklow HW, Gragson TL, Gries C, Hamilton SK, McGuire AD, Moore JC, et al. 2012. Long-term ecological research in a human dominated world. *BioScience* 62:342–353.
- Schadt CW, Martin AP, Lipson DA, Schmidt SK. 2003. Seasonal dynamics of previously unknown fungal lineages in tundra soils. *Science* 301:1359–1361.
- Schmidt SK, King AJ, Meier CL, Bowman WD, Farrer EC, Suding KN, Nemergut DR. 2014. Plant–microbe interactions at multiple scales across a high-elevation landscape. *Plant Ecology & Diversity* 8: This volume.
- Seastedt TR, Bowman WD, Caine TN, McKnight D, Townsend A, Williams MW. 2004. The landscape continuum: a model for high elevation ecosystems. *Bioscience* 54:111–121.
- Seok B, Helmig D, Williams MW, Liptzin D, Chowanski K, Hueber J. 2009. An automated system for continuous measurements of trace gas fluxes through snow: an evaluation of the gas diffusion method at a subalpine forest site, Niwot Ridge, Colorado. *Biogeochemistry* 95:95–113.
- Sherrod SK, Seastedt TR. 2001. Effects of the northern pocket gopher (*Thomomys talpoides*) on alpine soil characteristics, Niwot Ridge, CO. *Biogeochemistry* 55:195–218.

- Sherrod SK, Seastedt TR, Walker MD. 2005. Northern pocket gopher (*Thomomys talpoides*) control of alpine plant community structure. *Arctic, Antarctic and Alpine Research* 37:585–590.
- Smil V. 2001. *Enriching the Earth: Fritz Haber, Carl Bosch and the Transformation of World Food Production*. Cambridge (MA): MIT Press.
- Spasojevic MJ, Bowman WD, Humphries HC, Seastedt TR, Suding KN. 2013. Changes in alpine vegetation over 21 years: are patterns across a heterogeneous landscape consistent with predictions? *Ecosphere* 4:art117.
- Steffen W, Crutzen PJ, McNeill JR. 2007. The Anthropocene: are humans now overwhelming the great forces of nature? *AMBIO: A Journal of the Human Environment* 36:614–621.
- Steltzer H, Bowman WD. 1998. Original Articles: Differential Influence of Plant Species on Soil Nitrogen Transformations Within Moist Meadow Alpine Tundra. *Ecosystems* 1:464–474.
- Suding KN, Ashton I, Bechtold H, Bowman W, Mobley M, Winkleman R. 2008. Plant and microbe contribution to community resilience in a directionally changing environment. *Ecological Monographs* 78:313–329.
- Townsend AR, Howarth RW. 2010. Fixing the global nitrogen problem. *Scientific American* 302:64–71.
- Williams MW, Baron J, Caine N, Sommerfeld R, Sanford R. 1996. Nitrogen Saturation in the Rocky Mountains. *Environmental Science & Technology* 30:640–646.
- Williams MW, Cline D, Hartman M, Bardsley T. 1999. Data for snowmelt model development, calibration, and verification at an alpine site, Colorado Front Range. *Water Resources Research* 35:3205–3209.
- Williams MW, Helmig D, Blanken P. 2009a. White on green: under-snow microbial processes and trace gas fluxes through snow, Niwot Ridge, Colorado Front Range. *Biogeochemistry* 95:1–12.
- Williams MW, Hood E, Molotch N, Caine N, Cowie R, Liu F. 2015. The ‘teflon basin’ myth: hydrology and hydrochemistry of a seasonally snow-covered catchment. *Plant Ecology & Diversity* 8: This volume.
- Williams MW, Losleben M, Hamann H. 2002. Alpine areas in the Colorado Front Range as monitors of climate change and ecosystem response. *Geographical Review* 92:180–191.
- Williams MW, Seibold C, Chowanski K. 2009b. Storage and release of solutes from a subalpine seasonal snowpack: soil and stream water response, Niwot Ridge, Colorado. *Biogeochemistry* 95:77–94.
- Williams MW, Tonnessen KA. 2000. Critical loads for inorganic nitrogen deposition in the Colorado Front Range, USA. *Ecological Applications* 10:1648–1665.
- Yuan X, Knelman JE, Gasarch EI, Wang D, Nemergut DR, Seastedt TR. *Forthcoming*. Plant community and soil chemistry responses to long-term nitrogen inputs drive changes in tundra bacterial communities.